

EFFICACY OF SIMPLE VIABILITY MODELS IN ECOLOGICAL RISK ASSESSMENT: DOES DENSITY DEPENDENCE MATTER?

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Abstract. One commonly used PVA (population viability analysis) approach applies a diffusion approximation (DA) of population growth to time series of abundance data to estimate population parameters and various metrics of extinction risk. The simplest versions of this PVA assume density-independent population growth, an assumption that is commonly called into question for populations experiencing self-limitation. Using time series data generated from simulations of populations limited by three commonly used forms of density dependence (ceiling, Beverton-Holt, and Ricker) we asked the question: “When do simple density-independent PVA models provide useful guidelines for prioritizing extinction risk despite density-dependence inherent in the underlying real populations?”

Simple DA methods severely underestimated maximum growth rates (μ_{\max}) used to generate time series data for all three forms of density dependence. These methods also underestimated the intrinsic environmental variability in growth rates, or process error (σ^2), for the ceiling model, but overestimated this parameter for the Beverton-Holt and Ricker models. Despite misestimation of the intrinsic parameters, the estimated probabilities of 50% and 75% declines were highly correlated with the observed probabilities for populations growing with a ceiling (coefficients of correlation, or $R^2 = 0.87$ – 0.93). DA methods were less accurate for populations exhibiting more complex forms of density dependence ($R^2 = 0.61$ – 0.79). Although correlations between observed and estimated risks were high, bias (e.g., over- and underestimation) was extensive. Estimated probabilities of 50% declines were typically much lower (overly optimistic) than observed probabilities of the same decline. By contrast, accuracy increased substantially for predictions of 75% decline, and the “optimistic” bias was replaced by conservative bias (overestimates of risk).

Regardless of the form of density dependence, estimates of risk were least accurate when populations were recovering rapidly but were much more accurate when most needed by conservation practitioners: when the population fluctuated near its carrying capacity, recovered slowly to this abundance level, or declined toward extinction. Finally, when we classified risk in broad categories (e.g., extremely low, low, moderate, high, and extremely high), DA methods correctly or conservatively estimated the risk of a 75% decline for >85% of the parameter combinations, regardless of the form of density dependence followed by the real population.

Key words: density dependence; diffusion approximation; extinction risk; population viability analysis; time series.

INTRODUCTION

The limitations and challenges of population viability analysis (PVA) are widely appreciated (Boyce 1992, Reed et al. 2002). Among the challenges most extensively discussed in the literature are the difficulty of estimating parameters when data are sparse (Dennis and Taper 1994, Taylor 1995), the bias introduced by sampling error on estimates of process error (Meir and Fagan 1999, Holmes 2001, De Valpine and Hastings 2002), difficulty in separating demographic and environmental sources of stochasticity from count data (En-

gen et al. 1998, Morris and Doak 2002), and the extraordinarily large confidence intervals around estimates of risk (Ludwig 1999, Fieberg and Ellner 2000). However, most of these problems stem from insufficient or imprecise observation.

A more fundamental challenge to PVA is that biological populations change through time according to processes that are rarely accurately captured by *any* population viability model. These processes include nonstationarity in environmental conditions (Beissinger 1995, Zeng et al. 1998, CRI 2000), individual differences in performance (Fox and Kendall 2002, Kendall and Fox 2002), and other forms of demographic stochasticity (Lande 1993) and self-regulation through density dependence (Dennis and Taper 1994, Foley 1994, Dennis et al. 2001). Of these complexities in population dynamics, density dependence has been

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more frequently reported in empirical studies (e.g., Gaston 1988, Stacey and Taper 1992, Kemp and Dennis 1993, Dennis and Taper 1994, Foley 1994). In this paper we explore whether or not a simple density-independent model for population growth can summarize useful features of a density-dependent population process in a way that might inform conservation priority setting.

The simple model that we choose to analyze is a PVA based on a diffusion approximation of exponential population growth with environmental stochasticity (Lande and Orzack 1988, Dennis et al. 1991). This particular diffusion approximation model (hereafter, “simple DA model”) yields maximum likelihood estimates of the mean population growth rate (μ) and the variance in this rate, or “process error” (σ^2), via simple linear regression (Dennis et al. 1991). These parameters can then be used to calculate the long-term population growth rate, λ , and a variety of risk metrics such as the mean time to extinction and the probability of decline to critical threshold levels.

Despite its simplicity and ease of use (e.g., Morris et al. 1999, Morris and Doak 2002), the simple DA model ignores density dependence, a potentially important population dynamic for a variety of threatened species (e.g., Stacey and Taper 1992, Foley 1994). The lack of density dependence in DA risk estimation has spurred considerable recent interest in developing more sophisticated, nonlinear models to estimate density-dependent population parameters (Dennis and Taper 1994, Foley 1994, Constantino et al. 1997, Dennis et al. 2001, De Valpine and Hastings 2002). With higher numbers of parameters to estimate, however, these advanced methods may require more data (longer time series) to achieve the same precision as simpler methods (Hilborn and Mangel 1997). Moreover, even when data are plentiful, density-dependent parameter estimation is much more numerically intensive than the simple regression model required to estimate parameters and risk using the DA method (Dennis et al. 2001, De Valpine and Hastings 2002).

Ultimately, advances in the ease of application of nonlinear stochastic models may provide practitioners with tools for predicting extinction risk that are more accurate, and as accessible as the linear (DA) model. Until these advances have been made, it is critical to quantify the accuracy of linear models at estimating risk for populations that experience nonlinear growth, not only for future analyses, but also for evaluating prior analyses using simple viability models assuming density independence. Finally, even after new advances, nonlinear models still require more data to achieve the same precision as linear models with fewer parameters. It will be important to identify the types of populations for which linear models yield accurate risk estimates despite nonlinear population growth. When accuracy is not sacrificed, models with fewer parameters to estimate should be preferred. Thus, the goal of

this analysis is to quantify the accuracy of the simple DA model at estimating risk for populations experiencing various forms of density dependence.

Specifically, we address three questions about the use of a simple DA model in risk classification. (1) How poor are extinction risk estimates generated from the simple DA model when populations experience density dependence? (2) For which types of populations (e.g., small but recovering vs. steadily declining) are estimates of risk from the simple DA model likely to be most affected by density dependence? (3) Can simple DA methods accurately rank populations in more general categories of risk (e.g., high, medium, low) despite density-dependent growth in real populations?

METHODS

To assess whether the simple DA model could still predict relative risk for populations experiencing density dependence, we generated 40-year time series of abundance data according to three different density-dependent processes and then estimated the parameters from the first half of the simulated data, assuming a simple density-independent DA model. From estimated parameters, we predicted the expected trajectory over the next 20 years and compared it to the trajectory actually observed. Our results are best interpreted by comparison to a control, in which we apply the simple DA model to time series generated according to exponential growth with lognormal process error. In this case, the simulated data meet all of the limiting assumptions of the simple DA model (Morris and Doak 2002), and we would expect the predicted and observed data to match. In each case, we compare the outcome from the real model (i.e., the model used to generate time series data) to the fate of the same populations as predicted by simple DA methods.

Models used to generate time series data

We used time series of abundance data generated by four discrete-time models of population growth: a density-independent model and three density-dependent models. In each case we added environmental variability—or process error—as a lognormal variate (following Dennis et al. 2001) and assumed no observation error. The density-independent model was (following Dennis et al. 1991):

$$N_{t+1} = N_t \exp(\mu + z) \quad z = \text{Normal}(0, \sigma^2) \quad (1)$$

where N_t is the population size at time t , μ is the mean annual growth rate, and z is the process error associated with this rate and has variance σ^2 . Time series data from this simulation model meet the assumptions for the simple DA viability model (Morris and Doak 2002).

By contrast, time series data from populations experiencing density dependence violate one key assumption of simple DA methods: that population growth is density independent. The three density-de-

pendent models that we used to generate simulated data were: the ceiling (Lande 1993, Akçakaya et al. 1999), Beverton-Holt (Beverton and Holt 1957, 1993, Ricker 1975), and Ricker (Ricker 1954, 1975) models. Populations growing according to a ceiling model experience density-independent dynamics below an upper threshold abundance, or ceiling, K , but do not exceed this abundance level, such that

$$N_{t+1} = \begin{cases} N_t \exp(\mu_c + z) & \text{for } N_t \exp(\mu_c + z) < K \\ K & \text{for } N_t \exp(\mu_c + z) > K \end{cases} \quad (2)$$

where μ_c is the maximum growth rate achieved only when the population size is lower than K . The ceiling model has been used extensively in conservation science to represent density-dependent population growth (Lande 1993, Middleton et al. 1995, Meir and Fagan 1999) and is one of several forms of density dependence available in packaged PVA software (e.g., RAMAS Space; Akçakaya et al. 1999). Models with dynamics similar to the ceiling model (e.g., "hockey stick" models) also have been advocated in fisheries science to describe the population growth of a variety of commercial fish species (Barrowman and Myers 2000, Bradford et al. 2000).

Beverton-Holt and Ricker models are more traditional representations of density dependence in fisheries stock assessment models (Hilborn and Walters 1992, Burgman et al. 1993, Getz 1996, Pascual et al. 1997, DeValpine and Hastings 2002). These models also have been incorporated into standard PVA software, e.g., RAMAS GIS 3.0 and RAMAS Metapop 3.0 (Applied Biomathematics 1998, 2001) to represent density dependence resulting from either contest (Beverton-Holt) or scramble (Ricker) competition (Akçakaya et al. 1999). These models differ from the ceiling model in two ways. First, the effects of density on the population growth rate occur over all abundance levels (not simply those greater than K). Second, in Ricker and Beverton-Holt models, high values of process error may force the population above its carrying capacity (K), leading to strong negative density-dependent feedback and, consequently, abundance levels much lower than K in the following year. This "overcompensation" for good years does not occur in time series generated by a ceiling model because the population is always reset to K during these good years (Fig. 1). Third, the Ricker formulation of density dependence produces damped oscillations (for $1 < \mu < 2$) and sustained two-period oscillations (for $\mu > 2$) even in the absence of process error (Fig. 1). Thus, at high growth rates, populations experiencing Ricker-type density dependence can exhibit variability from both intrinsic (deterministic) and extrinsic (stochastic) sources. Overcompensation and intrinsic cycling occur independent of process error and, therefore, should seriously corrupt risk estimates from simple DA methods that assume that all variability arises from interannual process variability (e.g., environmental stochasticity).

The Beverton-Holt model can be written as

$$N_{t+1} = \exp(\mu_b + z) K N_t / (\exp(\mu_b) N_t - N_t + K) \quad (3)$$

where μ_b is the maximum growth rate experienced by populations growing according to Beverton-Holt dynamics, and all other variables are defined as in Eq. 2. The Ricker model is expressed as

$$N_{t+1} = N_t \exp(\mu_r - b N_t + z) \quad (4)$$

where μ_r is the maximum population growth rate for populations growing according to Ricker dynamics, and $b = |\mu_r|/K$ is the effect of density on this maximum growth rate. For the parameter b , the absolute value of μ_r is used, rather than simply μ_r , common in more traditional versions of the Ricker model. The traditional formulation produces biologically unrealistic behavior for $\mu_r < 0$ (specifically, $b N_t < 0$, and N_{t+1}/N_t higher for populations closer to K). Because we were interested in evaluating the performance of the simple DA in evaluating risk for declining populations (i.e., $\mu_r < 0$), we use $b = |\mu_r|/K$ to circumvent this pathological behavior. Finally, note that the Ricker model as expressed in Eq. 4 is identical to logistic models more commonly used to represent density dependence for noncommercial species (e.g., Stacey and Taper 1992).

We generated time series for each model using values of μ_{\max} (e.g., μ_c , μ_b , or μ_r) between -0.5 and 2.0 (increments of 0.1), and σ^2 between 0 and 2.0 (increments of 0.1). Populations with positive underlying dynamics (increasing) have $\mu_{\max} > 0$ and declining populations have $\mu_{\max} < 0$. In the density-independent model, all values of μ and σ^2 were replicated across four starting population sizes ($N_0 = 10, 100, 1000$, and 10000). In density-dependent models, we used four values of K ($100, 1000, 10000$, and 100000) and six values of N_0 , corresponding to $1, 10, 25, 50, 75$, and 100% of the ceiling or carrying capacity. This was done to assess the contribution of both ceiling height, K , and the ratio of the starting population size to the ceiling, N_0/K , to error in risk assessment associated with density dependence. In all cases, parameter values used in simulation models were chosen to encompass the range of values estimated from a variety of representative animal species (Table 1) and a range of possible model behavior (e.g., damped oscillations in the Ricker model). For all models, we generated 1000 40-year stochastic realizations for each parameter combination (2080 and 12480 parameter combinations for density-independent and density-dependent models, respectively).

Comparison of DA estimates for exponential vs. density-dependent processes

We divided the time series into a fitting interval (years 1–20) and an observation interval (years 21–40). We then estimated the population growth rate (μ') and process error (σ'^2) during the fitting interval using the simple DA model (Dennis et al. 1991, Morris et al.

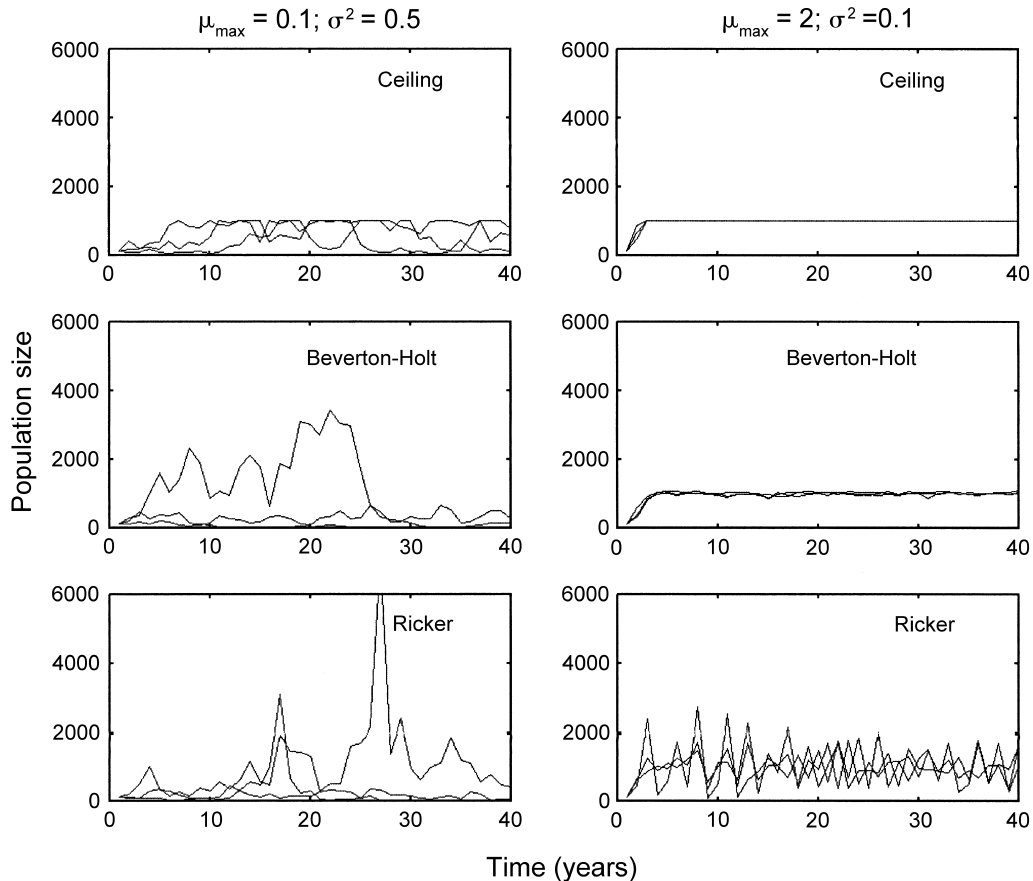


FIG. 1. Sample time series showing overcompensation (spikes in left panels) for Beverton-Holt and Ricker (but not Ceiling) models and intrinsic cycling (coupled with low levels of process error) in the Ricker (but not Beverton-Holt or Ceiling) models (right panels). Values used for the parameters μ_{\max} and σ^2 were identical for each model but differ between columns of panels.

1999). Using our estimates of these demographic parameters, we then estimated the probability of a population declining to two threshold abundance levels (“quasi-extinction thresholds”) over the observation interval. These thresholds were 50% (P'_{50}) and 75% (P'_{75}) of the population size at the end of the fitting interval. Quasi-extinction thresholds are relatively straightforward to calculate using μ' and σ'^2 , and they are one of several metrics currently used to identify populations and species of special concern by the IUCN (2000).

Several authors provide analytical solutions for P'_{50} and P'_{75} (e.g., Lande and Orzack 1988, Dennis et al. 1991) based on DA estimates of μ' and σ'^2 ; however, these solutions are for a process that is observed continuously. In our simulated data, we observe the process only at discrete, one-year intervals. Probabilities of a given decline for a process observed at discrete intervals are lower than analytical solutions for the same probabilities for continuous observations (e.g., Lande and Orzack 1988, Dennis et al. 1991). Analytical solutions for P'_{50} and P'_{75} for one discrete observation in the future (e.g., year 21) are relatively straightforward

(E. Holmes, *unpublished data*), but become much less tractable for multiple observations. To circumvent this problem, we calculate P'_{50} and P'_{75} numerically using the DA estimates of growth parameters (e.g., via Monte Carlo methods).

To quantify the efficacy of simple DA methods at predicting population growth parameters for the density-dependent processes, we plotted the true values of the vital rates—those used to generate initial time series data (μ_{\max} and σ^2)—against the median values of the DA estimates of these parameters (μ' and σ'^2) from each 1000 time series replicates for each parameter combination. Similarly, to evaluate the effect of density dependence on predictions of 50% and 75% declines, we compared median estimates of these probabilities (P'_{50} and P'_{75}) to the observed frequencies of these declines (P_{50} and P_{75}) over the observation intervals (years 21–40) of the original 40-year time series. These comparisons were done for all four models. Throughout this paper, we compare the efficacy of DA methods at estimating *maximum* growth rates in populations generated by simulation models in which maximum rates are *always* achieved (density-independent process) or

TABLE 1. Representative values of model parameters estimated from real populations.

Species	Fitted model	μ^\dagger	$K^\ddagger (\times 10^{-2})$	σ^2	Reference
Acorn Woodpecker	ceiling	0.22	0.52	0.061	Stacey and Taper (1992)
	Ricker§	0.563	0.3	0.047	Stacey and Taper (1992)
California Condor	exponential ^{DA}	-0.077	NT	0.12	Dennis et al. (1991)
Checkerspot butterfly	ceiling	0.22 ^L	46.29	0.65	Foley (1994)
Chum salmon	Ricker	0.37	5.97	0.079	Ricker (1975)
Cod	Ricker	1.77	0.95	0.32	Ricker (1975)
Elk (Teton)	Ricker	0.73	14.8	0.05	Dennis and Taper (1994)
Elk (Yellowstone)	Ricker	0.47	113.52	0.005	Dennis and Taper (1994)
Grizzly bear	exponential ^{DA}	-0.007	NT	0.009	Dennis et al. (1991)
	exponential ^{DA}	0.04	ND	0.015	Dennis and Taper (1994)
	ceiling	0.02 ^L	0.579	0.004	Foley (1994)
Insects: Orthoptera	Ricker	0.31–0.45	0.048–0.059	0.18–0.38	Kemp and Dennis (1993)
Insects: Anoplura	exponential	0.111	NT		Gaston (1988)
Insects: Coleoptera	exponential	0.07‡	NT		Gaston (1988)
Insects: Diptera	exponential	0.197‡	NT		Gaston (1988)
Insects: Hemiptera	exponential	0.279‡	NT		Gaston (1988)
Insects: Hymenoptera	exponential	0.22‡	NT		Gaston (1988)
Insects: Lepidoptera	exponential	0.12‡	NT		Gaston (1988)
Insects: Orthoptera	exponential	0.012	NT		Gaston (1988)
Insects: Psocoptera	exponential	0.225‡	NT		Gaston (1988)
Insects: Thysanoptera	exponential	0.26	NT		Gaston (1988)
Kirtland's Warbler	exponential ^{DA}	-0.02	NT	0.016	Dennis et al. (1991)
Laysan Finch	exponential ^{DA}	-0.001	NT	0.37	Dennis et al. (1991)
Mountain lion	ceiling	0.035 ^L	10.55	0.014	Foley (1994)
Palila	exponential ^{DA}	0.077	NT	0.22	Dennis et al. (1991)
Puerto Rican Parrot	exponential ^{DA}	0.034	NT	0.013	Dennis et al. (1991)
Red kangaroo	Ricker	0.117	1986.4	0.057	McCarthy (1996)
Salmon	exponential ^{DH}	-0.07	ND	0.09	McClure et al., unpublished data; CRI (2000)
Whooping Crane	exponential ^{DA}	0.005	NT	0.014	Dennis et al. (1991)
Wolf	ceiling	0.04 ^L	4.2	0.32	Foley (1994)

Note: Abbreviations are as follows: DA, fitted by simple DA (following Dennis et al. [1991]); DH, fitted by modified DA, or Dennis-Holmes method (following Holmes [2001]); L, based on annual growth rates ($\mu_c = N_{t+1}/N_t$ where $N_t < K$; ND, not detected by bootstrap likelihood ratio test (Dennis and Taper 1994); NT, not tested.

$\dagger \mu_r = \ln(a)$, $K = \ln(a)/b$, where a and b are the growth parameters from Ricker models.

\ddagger Average of more than one taxon; see Gaston (1988).

\S Data fit to logistic model: $N_{t+1} = N_t e^{r(1/N_t/K)}$.

achieved only at certain abundance levels (density-dependent processes). Thus, DA growth rate estimates are inherently biased for density-dependent processes; however, the magnitude and direction of this bias are potentially informative for interpreting any bias in the estimation of risk.

Simple DA models, which assume a density-independent, stochastic population process with lognormal process error, should produce both accurate and relatively precise estimates of growth parameters (μ' and σ'^2) and risk for populations meeting these assumptions, given adequate sample size. The null hypothesis for the density-independent model is that estimated and observed values of these variables should be nearly equal. Thus if we plot the estimated vs. observed values, they should fall on a line with a slope of 1.0 and intercept of 0. We used deviations from this 1:1 relationship to evaluate the effects of density dependence on estimates of growth parameters and risk for the ceiling, Beverton-Holt, and Ricker models.

RESULTS

DA estimates of μ_{\max} and σ^2

As expected, estimated growth rates, μ' , and process error, σ'^2 , were accurate for time series generated by

the exponential model (Fig. 2). Real and estimated values of both parameters for populations growing exponentially tracked the 1:1 line very closely, with the exception of process error at large values of σ^2 (a result that would most likely improve with higher sample size).

By contrast, the DA model was generally unable to accurately estimate μ_{\max} or σ^2 in any density-dependent model. Maximum growth rates (μ_c , μ_b , μ_r) for time series generated by ceiling, Beverton-Holt, and Ricker models were typically underestimated, except at values less than zero (e.g., declining populations; Fig. 2). As we have noted, the inability of the DA model to estimate μ_{\max} is not surprising. When μ_{\max} was very high in the density-dependent models, the simulated populations fluctuated about the carrying capacity and the apparent population growth rate was stable ($\mu' = 0$), as seen in Fig. 2. Differences in the level of process error estimated from the density-dependent simulations were similarly striking (Fig. 2, right panels). DA methods underestimated the underlying process error for the ceiling model, but most severely overestimated this parameter for data generated by both Beverton-Holt and Ricker models. For all three density-dependent

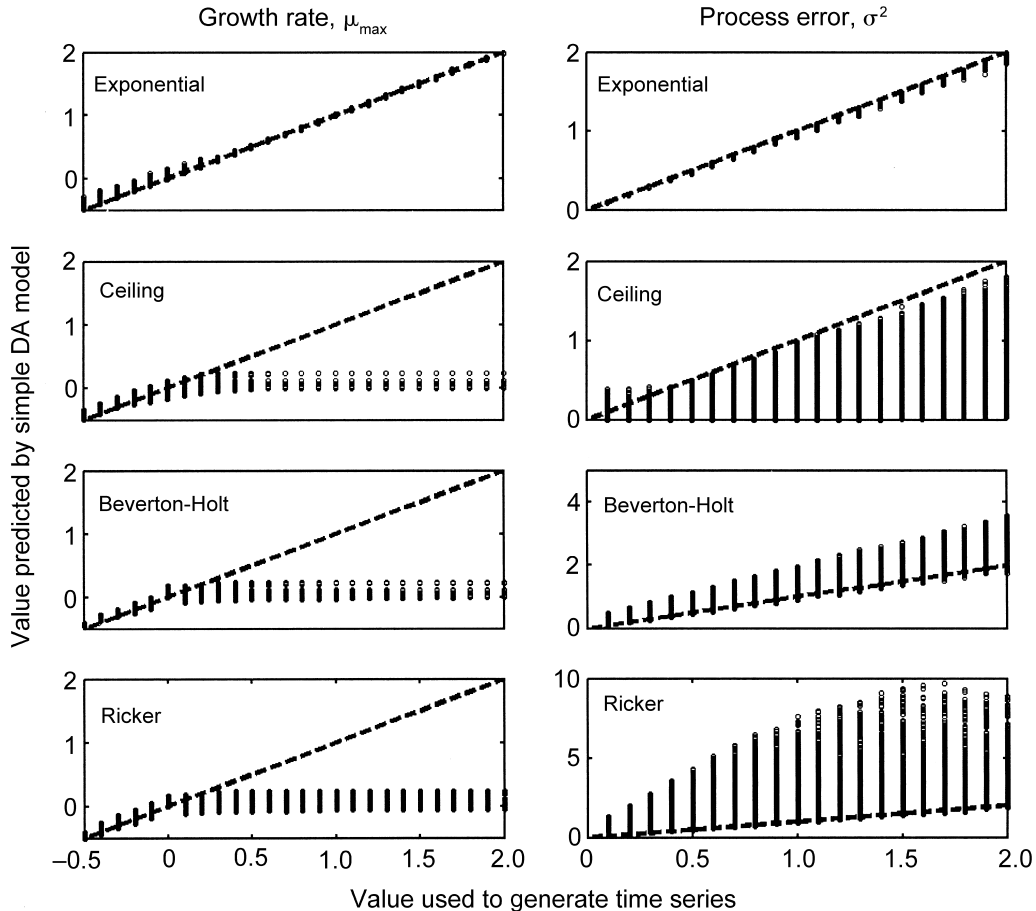


FIG. 2. Estimating growth parameters. The figure shows the relationship between parameter values used in simulations to generate time series data (x -axis: μ_{\max} , left panels; σ^2 , right panels) and values of these parameters estimated by a simple DA viability model (y -axis: μ' , left panels; σ'^2 , right panels). Time series were generated according to four models of population dynamics: density-independent or exponential, ceiling, Beverton-Holt, and Ricker. Each point represents a median value of estimates from up to 1000 replicate simulations for a given set of parameter values, excluding combinations that produced <500 replicate time series that did not go extinct ($N \leq 1$) within the fitting interval ($t = 1-20$).

models, DA estimates of process error (σ'^2) were extremely variable for a given value of “real” process error (σ^2). Overestimation of process error in Beverton-Holt and Ricker time series probably results from “overcompensation error,” i.e., an interaction between process error (stochastic overshooting of K) and density dependence (e.g., Fig. 1). In both models, overshooting is most often followed by a sharp decline in abundance due to density dependence, thereby inflating the variability of the population as perceived by DA methods. In addition to a feedback between process error and stochasticity, process error estimates are probably inflated for time series generated by Ricker models at high growth rates, due to damped deterministic cycles inherent in populations with high intrinsic growth rates ($1 < \mu_r < 2$).

Predicting the risk of decline for populations experiencing density dependence

Differences between predicted and underlying model parameters (e.g., μ and σ^2) should be expected for pop-

ulations experiencing density dependence because this population dynamic modifies the expression of these parameters in the actual population trajectories. A more important question then is whether the parameters and projections from the simple DA model adequately predict important aspects of risk for density-dependent populations, despite an assumption of density independence. To examine this question, we quantified how well the simple DA model predicted the probability of percentage declines in abundance.

Predictions of the probability of 50% and 75% declines again fell on, or near, the 1:1 line for time series generated by the density-independent model (Fig. 3, Table 2). This is the expected result, because these populations meet all assumptions made by simple DA methods. Predictions of P_{50} and P_{75} were less accurate for populations experiencing density dependence. Plots of estimated vs. observed probabilities of 50% decline showed considerable deviation from the 1:1 line for all density-dependent time series (Fig. 3). For the ceiling

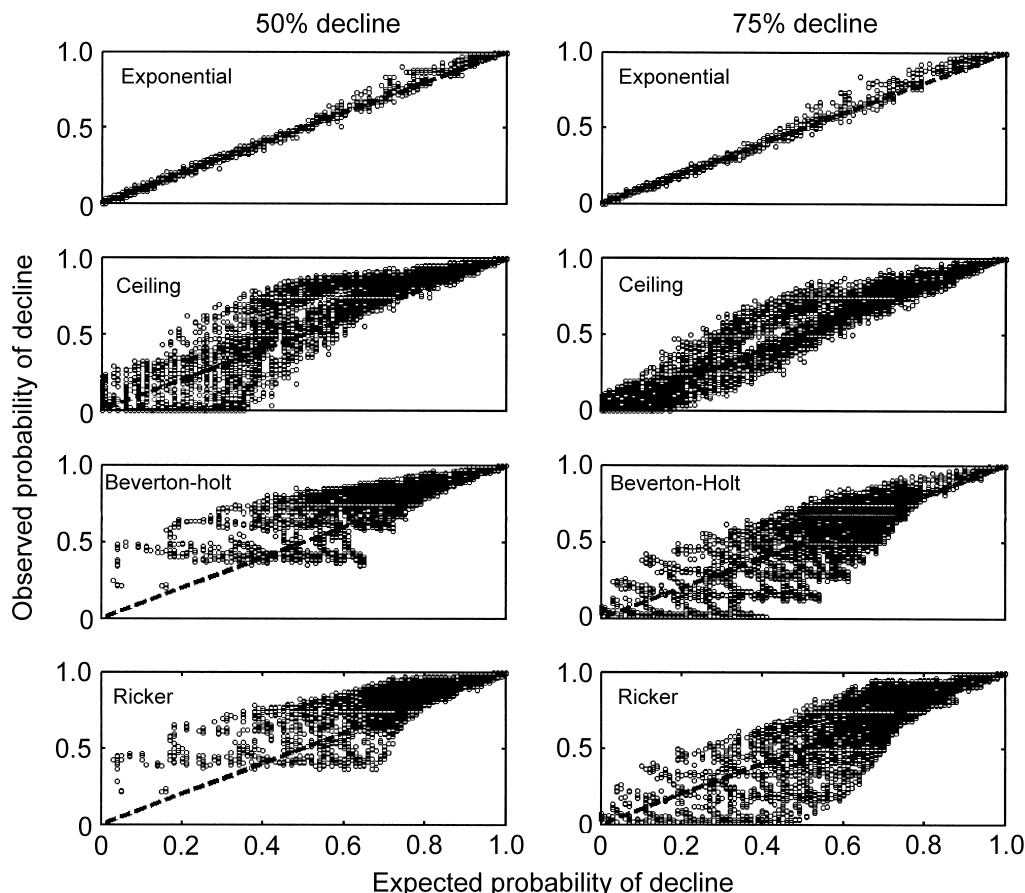


FIG. 3. Forecasting the risk of 50% and 75% declines. The plots show estimated (x-axis) and observed (y-axis) probabilities of 50% (left) and 75% (right) declines in abundance for time series generated by four models of population growth: density-independent or exponential, ceiling, Beverton-Holt, and Ricker. Each point represents a frequency of decline observed over the fitting interval for 1000 replicate time series (x-axis) and a median value of estimates from the fitting interval of the same time series (y-axis) derived from one parameter combination. Data include parameter values from full range (see *Methods*) that produced >500 replicate time series that did not go extinct ($N \leq 1$) within the fitting interval ($t = 1-20$).

model, predicted probabilities were frequently optimistic (i.e., predicted probability was lower than the observed probability). In Beverton-Holt and Ricker time series, this bias was much stronger; for most parameter values, observed P_{50} were at least 50%, but predicted P_{50} were generally much lower (Fig. 3). This suggests that the declines on the order of 50% are driven by variability due to density-dependent feedback and deterministic cycles in these two density-dependent processes, and that such declines are not adequately modeled as simple process error. Note that each point in Fig. 3 represents the median probability estimated from 1000 simulations with the *same* parameter values. Thus the wide range of variation between observed and predicted values of P_{50} (and P_{75}) in Fig. 3 results from different parameter values rather than variability in estimating these parameters (as in Fieberg and Ellner 2000).

In contrast to overly optimistic predictions of 50% declines for density-dependent populations, predictions of 75% declines were more accurate or conservative

than predictions of less severe declines. Predicted vs. observed probabilities fell on the 1:1 line with little variability for populations, limited only by a simple ceiling to growth (ceiling model; Fig. 3). For the Beverton-Holt and Ricker time series, the predicted vs. observed probabilities generally followed the 1:1 line, but with substantial variability about the line. In this case (P_{75}), bias was generally toward conservative predictions (e.g., where predicted P_{75} are higher than observed P_{75}). This result suggests that the overestimation of the intrinsic process error (Fig. 2) due to density-dependent feedback and deterministic cycles leads to an overestimation of severe declines. This is explored more fully in the next section.

The time series analyzed for Fig. 3 include populations with strong positive dynamics ($\mu_{\max} \gg 0$) and very high process error ($\sigma^2 > 1$). For real populations, however, values of σ^2 rarely exceed 0.5 (Table 1; Holmes 2001). Similarly, risk assessment is most often done on populations that appear to be declining ($\mu < 1$) or that fluctuate around low, but steady, density (μ

TABLE 2. Parameter estimates from regression of observed risk on risk estimated by DA methods for populations growing according to three density-dependent processes (ceiling, Beverton-Holt, and Ricker) across the full range of parameter space examined ("All space"; e.g., Fig. 3) and across a more limited range of parameter space ("Limited space"; e.g., Fig. 4; see *Methods*).

Model and risk of decline	Slope		Intercept		R^2	
	All space	Limited space	All space	Limited space	All space	Limited space
Exponential						
50%	0.95	0.98	0.0	0.004	0.99	0.99
75%	0.93	0.97	0.001	0.005	0.99	0.99
Ceiling						
50%	0.79	0.90	0.02	0.068	0.87	0.93
75%	0.83	0.90	0.03	0.04	0.92	0.95
Beverton-Holt						
50%	0.87	1.06	-0.13	0.03	0.61	0.70
75%	0.64	0.79	0.114	0.22	0.69	0.79
Ricker						
50%	0.81	0.97	-0.043	0.08	0.76	0.67
75%	0.66	0.73	0.165	0.25	0.66	0.73

Note: Risk is defined as the probability of a population declining to either 50% or 75% of the abundance at $t = 20$ years over the observation interval ($t = 21$ –40 years).

~ 0). When we limited the parameters examined in our analysis to this more practical range of growth rate and process error values (e.g., $\mu_{\max} < 1$, $\sigma^2 < 0.5$), we found that values of correlation coefficients between estimated and observed probabilities of 50% and 75% declines increased substantially for all density-dependent models (Table 2). In particular, risk estimates were substantially more accurate for time series generated by a ceiling model (Fig. 4). For the Beverton-Holt and Ricker models, the relationship between predicted and observed probabilities improved, but was still highly variable, especially when the expected risk was low. Interestingly, there was less predictive bias when the true risk of 50% or 75% decline was high (> 0.75). This suggests that the DA predictions were generally most accurate for the most at-risk populations.

Proximity to K and the predictive accuracy of simple DA methods

Although the simple DA model incorrectly estimated the observed probabilities of decline for some parameter combinations in density-dependent simulations, this simple model performed well for a wide range of parameter values (i.e., the data points close to 1:1 line in Fig. 4). In theory, estimates of risk should be least accurate for time series with dynamics that differ between the fitting and observation intervals, but should increase in accuracy as dynamics become more similar between these two intervals (Dennis et al. 1991). For populations experiencing density dependence, similarity in dynamics between these two intervals is most likely to be determined by the proximity of a population to the carrying capacity, or, more precisely, the time required for a population to reach this threshold abundance level.

To examine the effect of distance from carrying capacity on DA predictions, we calculated average times required for a population to reach the ceiling or carrying capacity:

$$\tau_K = x_K / |\mu_{\max}| \quad (5)$$

where x_K is the distance from the starting population size to carrying capacity on a log scale, or $\log(K/N_0)$. This metric provides an index for similarity between dynamics in the fitting and observation intervals. The extent to which the fitting interval predicts the behavior in the subsequent observation interval should be lowest when $\tau_K \rightarrow T_{\text{fit}}$, where T_{fit} is the time at the end of the fitting interval, but should increase either as $\tau_K \rightarrow 0$ or $\tau_K \rightarrow T_{\text{tot}}$, where T_{tot} is the time at the end of the entire time series. Hence, we hypothesized that errors in risk estimation should be highest when populations reach the carrying capacity near the end of the fitting interval ($\tau_K \approx 20$), and lowest when populations maintain a stochastic equilibrium density about the ceiling ($\tau_K \approx 0$) or simply do not reach the ceiling over the entire time series ($\tau_K \gg 20$).

Underestimation of the probabilities of 50% and 75% declines was most severe where $\tau_K > 0$ or $\tau_K < 20$, but was generally low (< 0.1) where $\tau_K > 20$ or $\tau_K \approx 0$ (Fig. 5). This indicates that the overly-optimistic risk estimates occurred mainly for those parameter combinations producing population trajectories reaching K at some point during the fitting interval. We observed this pattern regardless of the type of density dependence used to generate the time series.

By contrast, overestimation of the probabilities of decline (conservative risk estimates) did not vary consistently with τ_K , but instead depended strongly on the form of density dependence used to generate time series

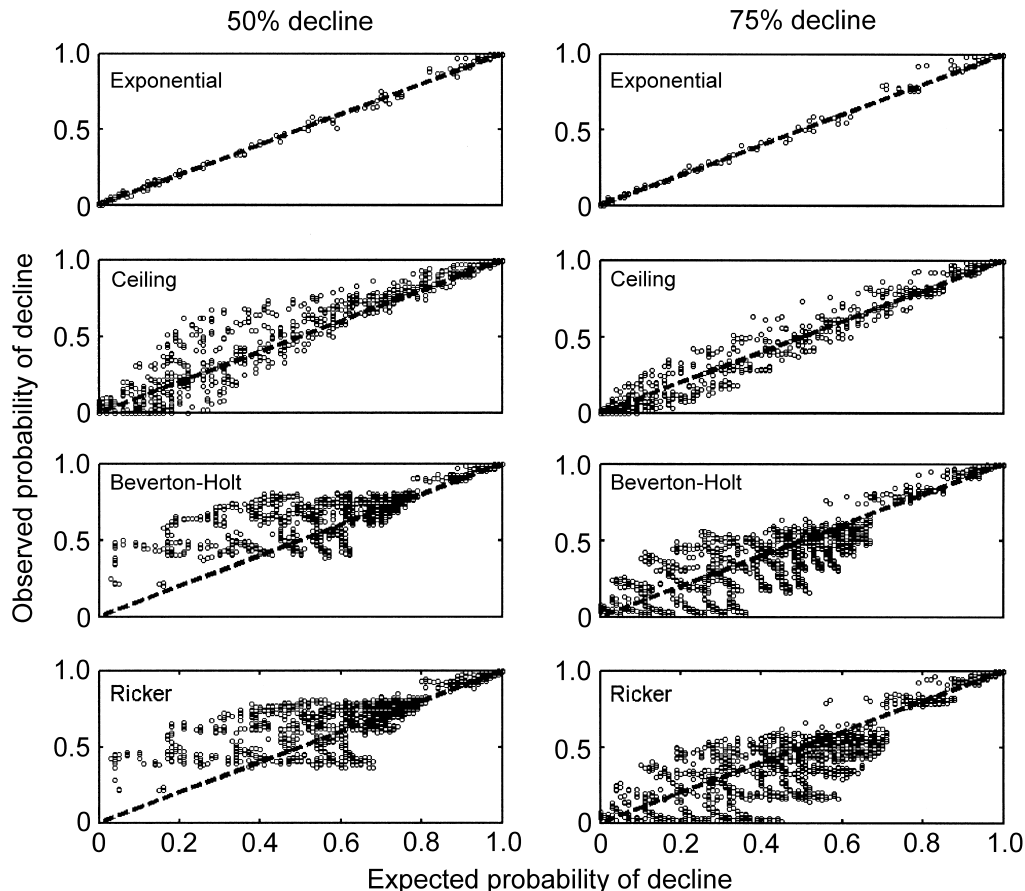


FIG. 4. Forecasting the risk of 50% and 75% declines when population growth and process error are relatively low. The plots show estimated (x-axis) and observed (y-axis) probabilities of 50% (left) and 75% (right) declines in abundance for time series generated by three models of population growth: density-independent or exponential, ceiling, Beverton-Holt, and Ricker. Each point represents a frequency of decline observed over the fitting interval for 1000 replicate time series (x-axis) and a median value of estimates from the fitting interval of the same time series (y-axis) derived from one parameter combination. Data include parameter values from a more limited range (see *Methods*) that produced >500 replicate time series that did not go extinct ($N \leq 1$) within the fitting interval ($t = 1-20$).

data (Fig. 6). Overestimation of risk was common in time series generated by a ceiling model when the initial population size was near K ($\tau_K = 0$), regardless of the value of process error experienced by experimental populations (Fig. 6). In Beverton-Holt and Ricker models, overestimation error was only encountered for populations with initial abundance levels very near carrying capacity and low values of process error (σ^2 ; Fig. 6). The narrower range of parameter values leading to risk overestimation in Ricker and Beverton-Holt models appears to be driven by two dynamics. First, in both Beverton-Holt and Ricker models, DA methods appear to misattribute process error to variability caused by feedback between density dependence and stochastic overshooting of the carrying capacity (e.g., overcompensation). Second, DA methods also misattribute process error to damped oscillations brought on by high growth rates, but only in the Ricker model.

In both Ricker and Beverton-Holt models, DA methods overestimate process error, which in turn leads to

overestimates of the risk faced by these populations. This result is expected from analytical solutions for P_{50} and P_{75} in which the probability of decline from a given initial abundance (N_0) to any quasi-extinction threshold (N_q) is equal to $(N_q/N_0)^{2\mu/\sigma^2}$ (cf. Dennis et al. 1991: Eq. 85). Thus, the estimated probability of any decline is inflated by a factor:

$$\varepsilon = (N_q/N_0)^{-2\mu e/(\sigma^2(\sigma^2+e))} \quad (6a)$$

such that

$$P'_{qe} = \varepsilon(P_{qe}) \quad (6b)$$

where ε is the proportional error in the estimate (P'_{qe}) of the true probability of a given decline (P_{qe}) and $e = (\sigma'^2 - \sigma^2)$, the difference between estimated and true process error. Analysis of individual time series indicates that overcorrection may lead to overestimation of process error and risk when populations have high variability relative to mean growth rates for populations growing according to Beverton-Holt and Ricker dy-

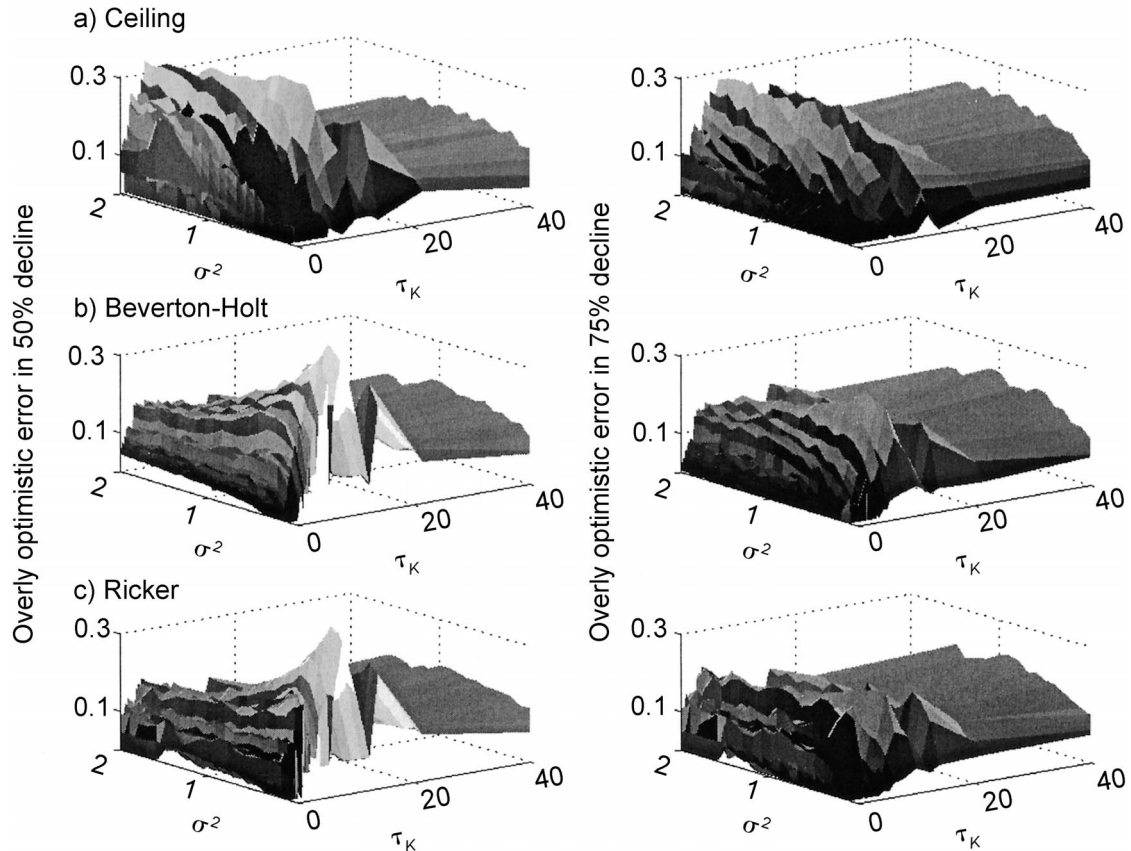


FIG. 5. The effect of process error (σ^2) and mean time to ceiling ($\tau_K = |x_K|/\mu$, where $x_K = \log(N_0/K)$) on the underestimation of risk, or “overly optimistic error” ($e = P_x - P'_x$, where $e > 0$) in predictions for the probabilities of 50% (left) and 75% (right) declines (P_{50} and P_{75}) for time series generated by a ceiling (top), Beverton-Holt (middle), or Ricker (bottom) models. Error values are averaged within each value of τ_K .

namics. Similarly, intrinsic cycling in populations limited by Ricker-type density dependence should lead to further corruption of process error estimates and overestimation of risk (J. L. Sabo, *unpublished data*).

Evaluating the effect of density dependence on the relative risk of extinction

In the context of real-world conservation settings, practitioners often are interested in comparing the relative risk of extinction faced by a handful of at-risk populations rather than estimating the absolute risk of a single population. For example, if funding permitted recovery efforts for only half of a group of 10 at-risk species, one might wish to determine which five species fall in the highest categories of risk. Moreover, a comparison of risk estimates from simple DA methods where risk is defined in broader categories (e.g., high vs. low) may be more robust to violations of key assumptions of these models. To address the effect of density dependence on predictions of the categorical risk from the simple DA model, we grouped estimates of quasi-extinction probabilities and observed frequencies of similar declines into five categories: extremely

low (0–20%), low (21–40%), intermediate (41–60%), high (61–80%), and extremely high (81–100%). We then classified categorical risk estimates as correct (estimated and observed risk in same category), conservative (estimated risk at least one category higher than observed risk), or overly optimistic (estimated risk at least one category lower than observed risk).

Simple DA methods correctly classified the risk of 50% and 75% declines for exponentially growing populations in 87% and 98% of the parameter combinations examined, respectively (Fig. 7). Classification was less accurate for density-dependent populations, but among these it was most accurate for the ceiling model. For populations growing according to a ceiling model, simple DA methods correctly classified P_{50} in 69% and P_{75} in 84% of the cases analyzed. The simple DA model more frequently classified risk incorrectly for populations growing according to Beverton-Holt and Ricker dynamics (Fig. 7); correct classification occurred for only 50–60% of all parameter combinations for either model at either risk level. However, most incorrect classifications for forecasts of 75% declines were conservative, such that the simple DA model provided either

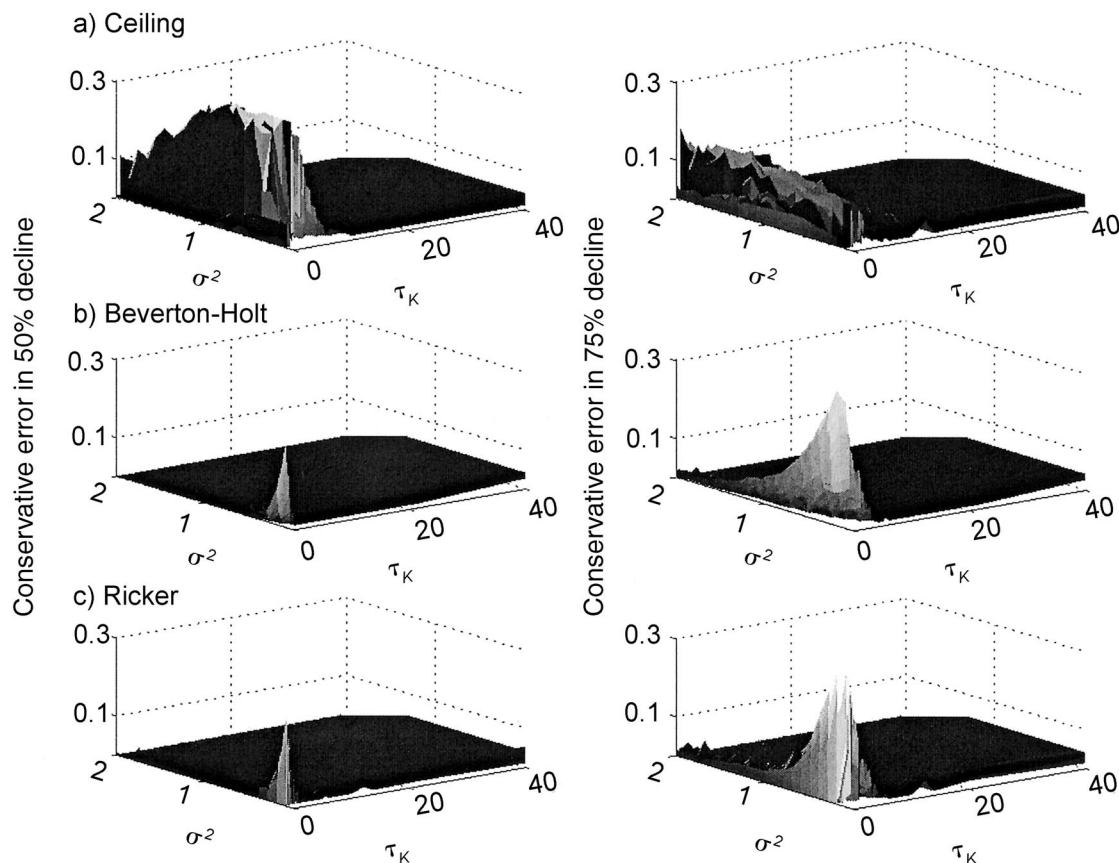


FIG. 6. The effect of process error (σ^2) and mean time to ceiling ($\tau_K = |x_K|/\mu$, where $x_K = \log(N_0/K)$) on the overestimation of risk, or "conservative error" ($e = P_y - P'_y$, where $e < 0$) in predictions for the probabilities of 50% (left) and 75% (right) declines (P_{50} and P_{75}) for time series generated by a ceiling (top), Beverton-Holt (middle), or Ricker (bottom) models. Error values are averaged within each value of τ_K .

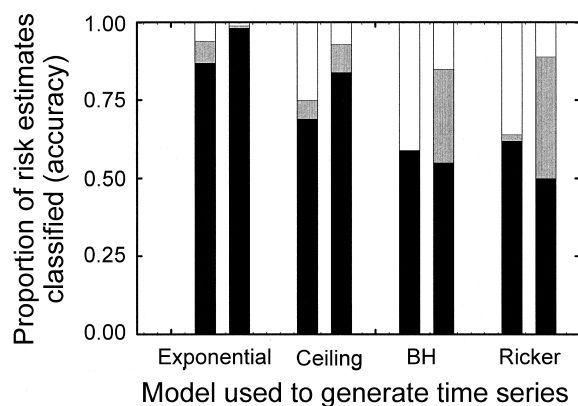


FIG. 7. Categorical risk classification. The proportions of risk estimates that were correct (black), conservative (gray), and overly-optimistic (white) for probabilities of 50% and 75% declines (left and right bars, respectively, for each pair) when estimated and observed risk were converted to five discrete categories of risk: extremely low (0–20%), low (21–40%), medium (41–60%), high (61–80%), and extremely high (81–100%).

correct or conservative categorical risk estimates for the probability of a 75% decline in 91%, 85%, and 89% of the parameter combinations for populations growing according to ceiling, Beverton-Holt, and Ricker processes, respectively. DA methods provided less conservative forecasts of the categorical risk of a 50% decline, producing overly optimistic estimates in 25%, 41%, and 36% of the parameter combinations examined (for the ceiling, Beverton-Holt, and Ricker models, respectively). In all cases, underestimation of categorical risk occurred most frequently for populations that were quickly increasing toward the carrying capacity during the fitting interval.

DISCUSSION

When using models to evaluate extinction risk, the most important factors governing the reliability of risk estimates typically include our certainty in parameters like the rate of population growth, environmental variability, and population size (Boyce 1992, Morris et al. 1999). Clearly, other factors, such as the form of density dependence, can play a major role in determining the dynamics of real populations. However, estimating

parameters can be difficult for stochastic density-dependent processes (Dennis and Taper 1994), and rarely are we likely to have either the quantity or quality of data necessary to parameterize these types of nonlinear population growth models in the real world. In this paper we show that a density-independent PVA model can still give reasonably apt assessments of relative risk for density-dependent population processes, and in fact can provide fairly accurate measures of absolute risk when density-dependent populations are either at abundance levels where density effects are not strong, or when the effects of density remain constant over a specified management time frame (e.g., across fitting and observation intervals). Interestingly, the performance of the simple DA model is best for populations most in need of viability assessment: highly fluctuating, declining, and slowly recovering populations.

Does density dependence affect the efficacy of simple viability models at classifying risk?

Our results suggest that simple DA methods that assume a density-independent stochastic process will provide adequate predictions about the probabilities of population decline, despite density dependence under four sets of circumstances. First, simple DA methods are less prone to underestimate risk when density dependence is manifested as a simple upper threshold (ceiling) to population growth than as a more complex, nonlinear form of population growth (e.g., Ricker and Beverton-Holt models; Figs. 2–3). Coefficients of correlation (R^2) between estimated and observed risk were typically 10–15% higher for the ceiling than for Ricker and Beverton-Holt models, regardless of risk level (P_{50} and P_{75}) or the range of parameters analyzed (Figs. 2–3, Table 2). Thus, the efficacy of simple DA methods at characterizing risk depends on the form of density dependence experienced by real populations.

That risk estimates were more robust for populations limited only by a ceiling is not surprising because the ceiling model generates population trajectories that meet all of the limiting assumptions of simple DA methods when the population is below the specified ceiling. By contrast, the simple DA model more often provided less reliable risk estimates for populations that experience other, more complex, forms of density dependence (e.g., logistic, Ricker, and Beverton-Holt). Threshold forms of density dependence, with dynamics similar to the ceiling model, are most often manifested by space limitation (e.g., nest site locations or settling space). For example, salmon may be limited by nesting substrate such that overcrowding leads to nest superimposition and decreased egg survival (Flemming and Gross 1992). Similarly, many bird species are limited by structural features (tree hollows) needed for nesting (Møller and Erritzoe 1996). Finally, many sessile marine invertebrates are limited by settling space for recruiting pelagic larvae (Grosberg and Levitan 1992). By contrast, population regulation by food limitation

can occur directly via scramble competition, as represented by the Ricker model, or indirectly as a result of behavioral mechanisms or contest competition, as represented by the Beverton-Holt model (Akçakaya et al. 1999). Simple DA methods most likely are not as effective at classifying risk for these types of species (e.g., cod, elk, wildebeest).

Second, risk estimates are more precise for severe than for modest declines. R^2 values for the relationship between estimated and observed risk were higher for P_{75} than P_{50} in all cases except for the Ricker model, analyzed across the entire parameter set (Table 2). Moreover, categorical risk estimates (low, medium, high) were more frequently correct (ceiling model) or conservative (Ricker and Beverton-Holt models) for P_{75} than P_{50} (Fig. 7). These results suggest that density dependence may have less severe effects on estimates of the probability of extreme declines.

Third, the accuracy of risk estimates from simple DA models declines as a result of intrinsic cycling at high growth rates (Ricker model) or as a result of strong feedback between stochastic overshooting of the carrying capacity and density dependence (Ricker and Beverton-Holt models). Simple PVAs attribute all of the variation in population abundance to environmental variability and assume that there are no cycles in the population process itself or interactions between environmental variability and density dependence (as in overcompensation). These models will thus overestimate process error for populations exhibiting cycles or overcompensation, leading to overestimates of risk. This is, in fact, what we observed in this study. Overly optimistic estimates of risk were observed most frequently for populations generated by models known to exhibit overcompensation or cycling (e.g., Fig. 1; Beverton-Holt and Ricker). Newer methods capable of separating these two sources of error (Holmes 2001, De Valpine and Hastings 2002, Holmes and Fagan 2002) would probably give better risk estimates for populations with a tendency to cycle.

Finally, the efficacy of simple DA methods at estimating risk for density-dependent population processes depends not only on how the population experiences density effects, but also on when these effects occur. Specifically, the proximity of a population to an upper threshold abundance level (ceiling or carrying capacity) can strongly influence accuracy in risk assessment. Not surprisingly, if the population reaches carrying capacity near the end of the period when parameters are estimated (i.e., the fitting interval), then simple DA methods will produce inaccurate risk estimates because the dynamics during the fitting period will be quite different than that during the subsequent observation period (Boyce 1992, Beissinger 1995). Indeed, error (most notably, underestimation) in risk estimation was typically high for populations initially below the ceiling but likely to reach this threshold before the end of the fitting interval (i.e., $0 < \tau_K < 20$; Fig. 5). By con-

trast, when the population was fluctuating about the carrying capacity during the fitting and observation periods, high overestimation errors tended to occur, but only for Beverton-Holt and Ricker type density dependence. Overall, estimation errors were lowest and were within 0.1 of the true probabilities for populations below carrying capacity and not likely to reach it in either the fitting or observation intervals ($\tau_K \gg 20$), and for populations with ceiling-type density dependence that were fluctuating stably near the carrying capacity.

These results have important practical implications for the use of simple PVAs in conservation planning. Assessments by simple DA methods are generally robust when they are most needed: for declining or slowly recovering populations and for most space-limited populations fluctuating near their upper threshold abundance level. Thus, although DA methods that explicitly include density dependence are available (e.g., Foley 1994, Dennis et al. 2001, De Valpine and Hastings 2002), evaluating the assumption that population dynamics remain consistent between the prediction and forecasting intervals may be more important than using these more accurate PVAs to estimate extinction risk.

General recommendations about PVAs based on simple DA methods

Based on these general findings, we recommend against using simple DA methods in two scenarios: (1) to estimate the probability of relatively modest declines in abundance (e.g., $<50\%$); and (2) to estimate the risk of decline for a threatened population showing strong signs of recovery. We further suggest caution in forecasting risk with simple DA methods for populations strongly regulated by food limitation and thus most likely to approximate either Ricker or Beverton-Holt dynamics. Risk estimates are more likely to be overly optimistic for these types of species compared to those that experience density dependence purely by space limitation, especially when forecasting a relatively modest decline. In all three cases, blind application of simple DA methods to forecast risk is likely to produce erroneous estimates of viability. In these cases, we advise application of multiple models (e.g., the DA and one or several density-dependent analogs) and a careful statistical evaluation of the appropriateness of each (Dennis et al. 1991). Finally, we note that our analysis pertains to situations in which *only* count data are available. In cases where more intensive monitoring programs provide capture-recapture or demographic data, estimation of parameters in nonlinear (e.g., density-dependent) models may be more straightforward and may provide more accurate forecasts of risk faced by threatened populations.

Conclusion

The ability of simple models to inform conservation planning hinges on the goal of viability modeling. Al-

though accurate estimates of risk are always desirable, many real-world applications of PVA require only an accurate assessment of the relative risk of extinction among a handful of populations. These applications include identifying both the most and least at-risk populations. Identifying the most at-risk populations can help to prioritize conservation efforts and guide limited resources to populations most in need of recovery. Similarly, estimates of relative risk can help to identify which populations are in the "best shape" and hence should be placed in a conservation portfolio (Groves et al. 2000). When the desired application of a PVA is to compare levels of relative risk among multiple populations, simple PVAs assuming the wrong population process may still provide a sufficiently informative answer in a wide variety of situations relevant to conservation.

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